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Comparative Sensitivity of Binucleate and Trinucleate Pollen to Ultraviolet Radiation: A.Theoretical Perspective

by

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Comparative Sensitivity of Binucleate and Trinucleate Pollen to Ultraviolet Radiation: A Theoretical Perspective

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ABSTRACT

Angiosperm pollen shed in the binucleate condition (which is the case for most species) may be more susceptible to UV radiation damage than pollen shed in the trinucleate condition. This speculation is supported by data summarized from the literature which show that trinucleate pollen is more physiologically advanced at the time when it is shed from the anther. The time course of germination, penetration of the stigma, and successful fertilization is thus more rapid in these trinucleate species. This results in less exposure to solar ultraviolet and consequently less damage should be expected. Experiments are needed to test the sensitivity of these pollen types *in vivo* and to evaluate the efficacy of possible repair mechanisms.

INTRODUCTION

Ultraviolet radiation is capable of damaging angiosperm pollen. For example, chromosome aberrations induced by ultraviolet radiation have been detected by cytological methods (Kirby-Smith and Craig 1957) and by noting the loss of marker genes in the seed produced (Stadler and Sprague 1936). Whether pollen in nature suffers chromosomal aberrations due to solar ultraviolet is not known. Floral parts provide substantial screening from solar UV-B (Flint and Caldwell 1983); thus, the potential for UV-induced chromosome aberrations and other nucleic acid damage exists between the time of dehiscence and when the pollen tube and the generative nucleus penetrate the stigma. Ultraviolet radiation may also decrease pollen germinability. Only limited data from *in vitro* experiments with pollen of temperate latitude origin are available. In species with binucleate pollen, germination is significantly inhibited only when ultraviolet radiation levels similar to those of equatorial latitudes at high elevations are administered to germinating pollen (Flint and Caldwell 1984). Whether pollen from plants native to low latitudes would show similar sensitivity is not known. Species with trinucleate pollen may be more resistant to ultraviolet damage (Pfahler 1981; Flint and Caldwell 1984), although only two species have been examined.

To investigate pollen sensitivity to UV-B radiation under conditions which are similar to a field situation is difficult and time consuming. Thus, perspective on the potential sensitivity of pollen of different species is useful in selecting species for intensive study. By synthesizing data in

the literature on physiological, developmental and protective characteristics of pollen, we are able to examine, from a theoretical perspective, the potential differences in germination inhibition between species which possess binucleate and trinucleate pollen. These data may also be used as a framework for the examination of mechanisms involved in UV damage to pollen.

SURVEY METHODS

Reports describing pollen physiology, the time course of pollen life history, and potential protective mechanisms were classified according to whether the species had binucleate pollen, trinucleate pollen, or an intermediate condition known as "advanced" binucleate pollen. The extensive survey of Brewbaker (1967) was used to classify species as to whether the pollen was binucleate or trinucleate, and the separation of some taxa into a phylogenetically "advanced" binucleate category was taken from Hoekstra and Bruinsma (1979).

In determining the time course of pollen life history (germination, stigma penetration, pollen tube growth, and fertilization), in vivo data were used wherever possible. The only in vitro data included in this tabulation were for time to germination and tube growth rate of the "advanced" binucleate species and for the intervals to protein synthesis. Time to "fertilization" should be considered only as an approximation because some are reported as time to reach the ovule, others as time to the micropyle, and others are calculated based on tube growth rate and length of the style. When more than one report existed for a particular species, the values were averaged and counted as one entry.

RESULTS AND DISCUSSION

In the extensive survey of Brewbaker (1967), 70% of all taxa shed their pollen in the binucleate condition, while the remaining 30% shed trinucleate pollen. This characteristic usually applies to an entire plant family; only 12% of the families surveyed by Brewbaker (1967) contain both pollen types. No decisive correlations have been discovered between pollen type and plant phenology, morphology, habit, or distribution. The "advanced" binucleate category was proposed by Hoekstra and Bruinsma (1979). As this category is based on physiological, rather than cytological characteristics of pollen, only Tradescantia and Impatiens taxa have thus far been placed in this group (Hoekstra and Bruinsma 1979). It is likely that a number of other species with binucleate pollen will also be placed in this category.

It has also long been known that the two cytological pollen types differ dramatically in some physiological characteristics. Binucleate pollen germinates under a broader range of in vitro conditions and retains its viability longer. The reactions preventing incompatible pollination in species with these two pollen types occur in different tissues (Brewbaker 1967). Subsequent experimental and physiological work has revealed potential differences between these two cytological pollen types that may influence their sensitivity to UV radiation.

At the time of dehiscence, binucleate pollen is typically less physiologically advanced than trinucleate pollen (Table 1). Binucleate pollen has not yet completed its second mitosis, and must develop its mitochondria and also conduct protein synthesis before germination can begin. Trinucleate pollen has completed its second mitosis and is physiologically prepared for germination since its mitochondria are developed and the necessary protein synthesis (Table 2) has been completed before dehiscence. This early completion of protein synthesis accounts for the lack of ribosomes in pollen of many trinucleate species. (Maize, an exception, has numerous ribosomes which may function primarily in the growth of the pollen tube through the exceedingly long style.) Thus, in trinucleate pollen there are fewer processes which may be susceptible to UV radiation damage, which suggests that germination of this pollen type may be less inhibited by UV radiation than binucleate pollen. Whether the presence of different metabolic pathways and respiration rates (Table 1) influences sensitivity to UV radiation is uncertain.

Because of the physiological factors discussed previously, dramatic differences exist between the two cytological pollen types in the time required for development (Table 2). Most species with trinucleate pollen complete the germination-to-fertilization process in a much shorter time interval than species with binucleate pollen. (Had we included binucleate taxa requiring months to effect fertilization, such as Corylus and Quercus [Kramer and Kozlowski 1979], this difference would have been more pronounced.) As germination and stigma penetration usually occur more rapidly in species with trinucleate pollen, there is a shorter period of exposure to sunlight and thus less time for damage to occur. (Trinucleate pollen of Brassica oleracea is unusual in that it germinated slower than any other species in Table 2.)

"Advanced" binucleate pollen shares some, but not all, of the characteristics of trinucleate pollen, thus sensitivity of this group to UV radiation would be expected to be intermediate. Development is rapid as in trinucleate pollen (Table 2), in part because mitochondria are developed at the time of dehiscence (Table 1). Other characteristics are less developed (Table 1). Mitotic division is arrested at dehiscence, as in binucleate pollen. In Tradescantia pollen, polyribosomes are present, supporting the idea that, unlike in trinucleate pollen, protein synthesis is necessary for germination. However, polyribosomes rather than free ribosomes suggest that this will occur more rapidly than in typical binucleate pollen. In Impatiens pollen, a lack of ribosomes suggests that protein synthesis has been completed before dehiscence, as in trinucleate pollen. This category should perhaps include some of the rapidly germinating binucleate species, e.g., Persea americana, 6 min (Sedgley 1977) and Pisum sativum, 5 min (Hoekstra and Bruinsma 1978). Overlap between the lag times for germination of the binucleate and trinucleate categories would then be less. The frequency of occurrence of "advanced" binucleate taxa among the angiosperms needs examination.

As pollen tubes grow for a short distance on the surface of the stigma before penetrating it, potential protective mechanisms may be important at this stage (Table 3). Some species with binucleate pollen have wet stigmas, while species with trinucleate pollen tend to have dry stigmas. As these stigmatic exudates contain UV-absorbing phenolic compounds (Martin 1970), pollen grains may be at least partly shielded from solar UV radiation shortly after landing on the stigma. In addition, binucleate pollen

Table 1. Physiological characteristics of binucleate, "advanced binucleate", and trinucleate pollen which may result in differential sensitivity to UV-B radiation.

Factor	Binucleate	"Advanced Binucleate"	Trinucleate	Reference
Presynthesized RNA	yes	yes	- a	3,8,9
Second mitosis	arrested at prophase when shed	arrested at prophase when shed	occurs hours to days before shed	1,2,8
Ribosomes	monoribosomes	polyribosomes or no ribosomes	few ribosomes[a] (e.g. Asteraceae)	6,10
Mitochondrial development at dehiscence	undeveloped	nearly complete	nearly complete	4
Alternative oxidase pathway	no	no	yes	7
Respiration rate	low	low	high	4,5,6

[a]While in trinucleate maize pollen both RNA (Mascarenhas et al. 1984) and polyribosomes (Hoekstra and Bruinsma 1979) are present, they most likely function primarily in the growth of the pollen tube through the exceedingly long style. Maize may not be representative of most trinucleate pollen.

References: 1. Brewbaker 1967; 2. Brewbaker and Emery 1962; 3. Frankis and Mascarenhas 1980; 4. Hoekstra 1979; 5. Hoekstra and Bruinsma 1975; 6. Hoekstra and Bruinsma 1979; 7. Hoekstra and Briunsma 1980; 8. Mascarenhas 1975; 9. Mascarenhas 1978; 10. van Went 1974.

Table 2. Developmental characteristics of binucleate, "advanced binucleate", and trinucleate pollen which may result in differential sensitivity to UV-B radiation.

Factor	Binucleate	"Advanced Binucleate"	Trinucleate	Reference
Interval to germination[a] (min)	6-120 n=8 md=27.5[b]	2-6 n=2	1-360 n=15 md=7	1
Interval to protein synthesis (min)[a]	10 n=2	2 n=1	negligible after dehiscence, n=2	2
Interval to stigma penetration (min)[a]	10-75 n=3 md=10	-	4.75-480 n=9 md=8.5	3
Interval to fertilization (hr)[a]	3.5-168 n=22 md=36	1-6 n=2	0.5-16 n=18 md=4.75	4
Rate of tube growth (mm hr^{-1})	0.1-4.6 n=18 md=0.8	0.65 n=1	0.6-35 n=10 md=4.6	5

[a]Time intervals begin with the arrival of the pollen grain on the stigmatic surface or the germination medium.

[b]md = median

Table 2 (continued)

References:

1. Ameele 1982; Brown and Shands 1957; Cass and Peteya 1979; Chandra and Bhatnagar 1974; Cresti et al. 1980; Dickenson and Lewis 1973; Ferrari et al. 1983; J. Heslop-Harrison 1979; J. Heslop-Harrison 1980; Y. Heslop-Harrison 1977; J. Heslop-Harrison et al. 1975a; Y. Heslop-Harrison et al. 1984; Hoekstra and Bruinsma 1978; Kroh and Linskens 1963; Owens and Horsfield 1982; Randolph 1936; Russell 1982; Sastri and Shivanna 1979; Sedgley 1977; Sedgley and Buttrose 1978; Wilms 1980; Zeven and Van Heemert 1970.

2. Hoekstra and Bruinsma 1979.

3. Brown and Shands 1957; Chandra and Bhatnagar 1974; Ferrari et al. 1983; Y. Heslop-Harrison 1977; J. Heslop-Harrison and Y. Heslop-Harrison 1981; J. Heslop-Harrison et al. 1975b; Hoekstra and Bruinsma 1978; McLean and Ivimey-Cook 1956; Mattsson 1983; Owens and Horsfield 1982; Sastri and Shivanna 1979; Wilms 1980.

4. Ascher and Peloquin 1966; Brown and Shands 1957; Chandra and Bhatnagar 1974; Chen and Gibson 1973; Clarke et al. 1977; Herd and Beadle 1980; Y. Heslop-Harrison 1977; Hoekstra and Bruinsma 1978; Hopping and Jerram 1979; Jalani and Moss 1980; Kho et al. 1980; Kramer and Kozlowski 1979; Kroh et al. 1979; Lange and Wojciechowska 1976; Lee 1980; Luxová 1967; Maheshwari 1949; Mulcahy et al. 1983; Pope 1937; Pundir 1982; Pundir et al. 1983; Reger and James 1982; Russell 1982; Sastri and Shivanna 1979; Sedgley 1977; Sedgley 1983; Sedgley and Scholefield 1980; Socias i Company 1976; Staudt 1982; Stephens and Quinby 1934; Stott 1972; Thompson and Liu 1973; Vasil 1960; Wilms 1974.

5. Ascher and Peloquin 1966; Buchholz and Blakeslee 1927; Chandra and Bhatnagar 1974; Chen and Gibson 1973; Currah 1981; Facteau et al. 1973; Gillissen and Brantjes 1978; J. Heslop-Harrison 1980; J. Heslop-Harrison 1982; Y. Heslop-Harrison 1977; Hoekstra and Bruinsma 1978; Hopping and Jerram 1979; Jensen and Fisher 1970; Kroh et al. 1979; Kwack 1965; Lee 1980; Maheshwari 1949; Mascarenhas 1978; Mulcahy et al. 1983; Pundir 1982; Pundir et al. 1983; Russell 1982; Sedgley 1983; Sedgley and Buttrose 1978; Staudt 1982; Van Herpen and Linskens 1981; Vasil 1960; Williams and Maier 1977; Wilms 1981.

Table 3. Characteristics possibly conferring differential protection from UV-R radiation: comparison of binucleate, "advanced binucleate", and trinucleate pollen.

Factor	Binucleate	"Advanced Binucleate"	Trinucleate	Reference
Elutable compounds	high	-	low	6
Stigma surface	both wet and dry	dry	usually dry	2
Pollen tube growth on surface of stigma	yes	-	yes	1,2,7,8,9
Photoreactivation of DNA damage	yes	-	yes	3,5
Dark repair of DNA damage	yes	-	-	4

References: 1. Cass and Peteya 1979; 2. Y. Heslop-Harrison and Shivanna 1977; 3. Ikenaga et al. 1974; 4. Jackson and Linskens 1978; 5. Jackson and Linskens 1979; 6. Kirby and Smith 1974; 7. Kroh et al. 1979; 8. Sedgley and Scholefield 1980; 9. Wilms 1980.

contains more readily elutable compounds than trinucleate pollen. These elutable compounds probably include UV-screening flavonoids, since they are localized on the surface of the pollen and are quickly released (Wiermann and Vieth 1983). However, the relative flavonoid contents of binucleate and trinucleate pollens remain to be verified experimentally. These factors may provide greater protection for binucleate pollen and possibly offset the effect of greater UV exposure accumulated during their slow development.

Repair mechanisms may also ameliorate UV-B damage to DNA. Photoreactivation of DNA damage has been shown to occur in both binucleate and trinucleate pollen grains while dark repair has only been demonstrated in binucleate pollen (Table 3). Whether the efficiencies of these two repair systems differ between binucleate and trinucleate pollen has never been examined.

This review of pollen characteristics, and their potential contributions to UV sensitivity, can serve as a useful framework for the selection of test species for further work. Nevertheless, a considerable physiological and morphological diversity exists within each pollen category and diverse response to UV radiation would not be unexpected.

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